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with the Author's kind
regards

INAUGURAL DISSERTATION
ON THE
NATURE OF RESPIRATION,
AND THE
EXTENT OF ITS CONNECTION WITH THE
NERVOUS SYSTEM.

SUBMITTED TO
THE MEDICAL FACULTY
OF THE
University of Edinburgh,

IN CONFORMITY WITH THE RULES FOR GRADUATION,

BY AUTHORITY OF THE
VERY REV. PRINCIPAL BAIRD,
AND WITH THE SANCTION OF
THE SENATUS ACADEMICUS,

BY
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"But breathless, as we grow when *feeling* most."—BYRON.

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TO

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GUY'S HOSPITAL, &c. &c.

TO WHOSE ARDUOUS EXERTIONS IN THE FIELD OF DISCOVERY, THE
SCIENCE OF PHYSIOLOGY OWES MUCH OF ITS CELEBRITY,

THIS ESSAY

IS RESPECTFULLY INSCRIBED,

AS A TESTIMONY OF ADMIRATION OF HIS EMINENT ABILITIES,
AND OF GRATITUDE FOR YEARS OF UNREMITTING
KINDNESS AND PARENTAL SOLICITUDE,

BY HIS AFFECTIONATE AND DUTIFUL NEPHEW,

THE AUTHOR.

TO
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FELLOW OF THE ROYAL COLLEGE OF PHYSICIANS,
PROFESSOR OF MATERIA MEDICA IN THE UNIVERSITY OF
EDINBURGH, &c. &c. &c.

In Grateful Acknowledgement
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IN THE COURSE OF HIS ACADEMICAL STUDIES, ~~AND~~ WHICH HAVE
CONTRIBUTED IN NO SMALL DEGREE
TO ENDEAR TO HIM THE RECOLLECTIONS OF HIS
ALMA MATER,

THE DEDICATION
OF THE
FOLLOWING PAGES
IS RESPECTFULLY OFFERED,
IN THE HOPE THAT THEIR NUMEROUS IMPERFECTIONS
MAY MEET WITH THAT INDULGENCE WHICH
EXALTED TALENT
SELDOM FAILS TO BESTOW ON A FIRST ATTEMPT AT
LITERARY COMPOSITION.



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FOR
BRANSBY BLAKE COOPER, ESQ. F. R. S.
SURGEON TO GUY'S HOSPITAL, LECTURER ON ANATOMY,
&c. &c.

IN WHOM,
WITH THE HIGHEST PROFESSIONAL ATTAINMENTS,
ARE UNITED
THOSE QUALITIES OF HEART
WHICH ENDEAR HIM TO ALL WHO KNOW HIM,

THIS PAGE IS,
BY PERMISSION,
RESPECTFULLY RESERVED,
BY HIS GRATEFUL PUPIL AND FRIEND,
THE AUTHOR.

ON THE
NATURE OF RESPIRATION,
AND THE
EXTENT OF ITS CONNECTION WITH THE
NERVOUS SYSTEM.

IN investigating the phenomena of living beings, as they are presented to us in the two organic kingdoms of nature, we find that they are all of them referable to one or other of the two following divisions, which may be designated respectively as the essential and the accessory.

The first class, as its name implies, comprehends all those functions which are indispensable to the life of the individual, or the preservation of the species. To the second class, on the contrary, may be referred all those numerous additional phenomena which tend to establish relations with the external world, independently of those necessary to mere existence, and which are destined to enlarge the individual's sphere of enjoyment as a moving and sentient being.

Phenomena belonging to the former class, are, of course, constantly present, and of uniform operation in every department of organic nature; the latter are of partial occurrence, varying in intensity and extent, intermitting in their exercise, and sometimes absent altogether.

It is observable, however, with respect to these accessory functions, that although, from their own nature and character, they are not absolutely indispensable to life, they are, nevertheless, so intimately connected with the essential functions in the more complicated structures in particular, that the cessation of the action of the former, is inevitably followed by the destruction of the latter.

The phenomena of respiration, which it is the object of this essay to investigate, furnish an excellent example of the relation which these two classes of functions may bear to each other, where we find that an operation, in itself essential to life, is rendered, by incidental circumstances, subservient to other actions of comparatively minor importance.

Before proceeding, however, to the consideration of the subject proposed, I shall endeavour, as far as possible, to embody, in the following definition, the extent of signification intended to be conveyed by the use of the term “Respiration.” By the term “respiration,” then, it is meant to express “that reciprocal action of the fluids of organised substances, whether animal or vegetable, upon the elastic medium in which they are placed, by means of which, certain material changes are effected in the constituents of each, the intermission of which, for a longer or shorter period, (varying according to circumstances), necessarily involves a dissolution of the organised structure, and a total cessation of those energies by which it was enabled to sustain, increase, and reproduce the textures and organs of which it was composed.”

It will be seen from this definition, that the continuance of respiration is held to be essential to life, and that its intermission for any protracted period, is held to be incompatible with those phenomena which constitute life; and although, *à priori*, the wonderful tenaciousness of existence exhibited by batrachian reptiles, might lead to a different conclusion, yet by a close attention to these facts, it will

probably be found, that the circumstances were still such as not entirely to preclude respiration, in the extended sense in which I have endeavoured to define it.

It appears, indeed, somewhat extraordinary, that the greater number of physiologists who have treated of the conditions necessary to respiration, have omitted to draw a line of distinction between the real function of respiration, as above defined, and the preliminary contrivances adopted for its exercise ; the former is uniform, or nearly so, throughout the two kingdoms of nature, the latter are infinitely varied, in proportion to the greater or less complication of structure exhibited in different departments.

From this want of discrimination, much confusion has arisen. In the human body, for example, the function of respiration has been held to be essentially dependent on nervous influence, whereas it is easily demonstrable that this function may continue to exist in those departments of nature, where, if we may judge from the total want of its ordinary phenomena, nervous influence is utterly unknown.

It will therefore be my object, in the following dissertation, to lay before the reader a comparative view of this function throughout the two kingdoms of nature, with a view of establishing the close analogy that exists in the essential process, notwithstanding the great diversity in the preliminary conditions. At the same time, I shall offer a few observations on the development of the nervous system in the respective classes, in order that we may arrive at some definite conclusion as to the nature and extent of its connection with the actual function of respiration on the one hand, and with its mechanical operations on the other.

Of Respiration in Cryptogamic Vegetables.

Although our knowledge of the functions of this interesting but obscure class of vegetable productions, is at present

so indefinite, that any remarks on the subject of their respiration may seem altogether conjectural, yet I cannot forbear offering a few general observations upon them, inasmuch as there is probably no class of substances endowed with vitality, over which the condition of the atmosphere exerts a more extensively modifying influence. Unlike those structures provided with a vascular apparatus, in which the influence of the atmosphere on their growth and nutrition is maintained only through the medium of a circulating fluid, these uncomplicated tissues appear to derive directly from that element, materials by which, not only is their external configuration essentially influenced, but which, in some instances at least, appear to be the sole *media* through which the “*pabulum vitae*” is supplied and renovated. Whence is it, for example, that the lichens, which encrust with their foliaceous or leprous disks the surfaces of naked rocks, derive the materials by which they are enabled to generate and fertilize their sporuliferous shields? Is it from the unyielding flint, or the rugged granite, whose surface they are destined to cover? The reverse surely admits of demonstration. Whence is it that we seek in vain for similar incrustations in the narrow crevices of rocks, or on the walls of subterranean caverns? Deprived of the fostering influence of light and air, we find that even these lichens, although, as it were, the very humblest efforts of vegetation, can no longer exercise their simple functions.* With regard to fungi, it is well known that they are frequently meteoric, springing up after storms, or in peculiar states of the atmosphere, with prodigious rapidity; and those who are acquainted with the process employed by gardeners, for obtaining the “*agaricus cam-*

* For the authenticity of this statement, see Professor Lindley's Introduction to the Natural System of Botany, page 331. “No lichen is ever developed in mines, caverns, or places deprived of light; on this account, their shields are rare in the fissures of mountains,” &c.

pestris," will find that, by the exposure of certain mixtures of organic and inorganic matters, to well known atmospheric conditions, the true edible mushroom may be obtained with complete certainty ; while, on the other hand, there is no class in which poisonous qualities are more easily generated, if the eudiometrical and hygrometric state of the atmosphere be not attended to.* The change of colour, which many of this class exhibit in the laminæ of their under surface, when connected with a corresponding change of property,† is another remarkable fact, and furnishes a further proof how much influence is to be ascribed to the atmosphere, in altering the conditions of fungi, since variation in the colour of plants (as has been ably shewn by Mr Ellis)‡ have a very close relation with changes in the condition of that fluid. In algæ, the influence of the atmosphere is of no less importance, if we may judge from the numerous vesicles with which their leafy expansions are everywhere studded. We find, likewise, that latitude, depth, currents, &c. influence the forms of algæ nearly in the same way as latitude, elevation, and station, affect those plants which are more perfect ; so that, immersed as they are in the depths of the ocean, we have reason to believe that the influence of the atmosphere is still required to enable them to retain, not only their properties, but their form. Some botanists are of opinion that the distinction of lichens and algæ depends only upon the different conditions of the atmosphere with respect to humidity ; and it is found that the inferior species of algæ, namely, the slimy deposits on moist stones, shady walls, &c. belonging to the genera *Palmella*, *Nostoc*, and the like, occupy precisely those situations where, from the deficiency of light, and

* Is this, or is it not, an example of equivocal generation ? I confess, I see no other method of explaining this wonderful phenomenon.

† Professor Christison's Lectures, MS. copy.

‡ Ellis on the Changes of Air in Respiration and Vegetation.

prevalence of humidity, lichens are never observed, although beyond these circumstances, there be no difference in the surfaces to which they are attached.

Of the cryptogamic plants of the division “*Phylloideæ*,” it is perhaps unnecessary to speak separately, inasmuch as there is reason to believe that, in those genera at least, which are provided with a vascular system, the respiratory function is carried on in a similar manner to that of phanerogamic vegetables. I cannot, however, omit to mention that, with regard to the respiration of the orders “*Filices*” and “*Lycopodia*,” the researches of geologists have laid before us a field of speculation replete with interesting enquiries. From these it would appear, that in those rocks of the earlier secondary strata anterior in date to the “coal formation,” fossil ferns and lycopodia have been discovered of a size and luxuriance to which these plants, as they now exist upon the earth, even under the most favourable circumstances, have been found rarely to attain. The difficulty of accounting for this prolific vegetation at a period of the earth’s formation, when, as far as geologists can determine, its crust was entirely destitute of carbonaceous materials, has led a very able and ingenious botanist* to infer, that the atmosphere must have been the source from which these vegetables derived their carbon, by decomposition of its carbonic acid; and surely when we connect the circumstance of their unusual luxuriance with the subsequent large deposition of carbon in the “coal formation,” it requires no very great effort of imagination to suppose, that at the time of the decay of these vegetables, the carbon thus abstracted from the atmosphere gave rise to the deposition of coal, while at the same period the eudiometrical state of that fluid became ameliorated, and fitted to support

* M. Adolphe Brongniart. See a paper in the “*Mémoires de l’Academie des Sciences*” for 1828, and Professor Alison’s Lectures, MS. copy.

the existence of animals whose fossil remains are then discovered to have first existed. The floating islands which are constantly forming in the lake Solfatara in Italy, exhibit a striking example of the luxuriance of vegetation in an atmosphere impregnated with carbonic acid. These islands consist chiefly of lichens and confervæ, which are rapidly generated by the decomposition of this gas as it escapes from the waters of the lake, with a violence which gives to them the appearance of ebullition.* In concluding these remarks on the class cryptogamia, I would only observe, that the influence of the atmosphere in many of its families, appears to act as a direct source of nutrition, and that where no such supply is yielded or required, its presence is still necessary for the continuance of the functions of self-preservation and reproduction.

Of Respiration in Phenogamic Vegetables.

In this department of our subject, our knowledge has been so much improved by the labours of Priestley,† Ingenhouz,‡ and Ellis,|| that we are enabled to proceed with more confidence and certainty to detail the changes which the atmosphere undergoes, and the influence of those changes upon the living vegetables themselves. It would far exceed the limits of this dissertation, to enter into details of the various experiments which have been made to determine these points; I shall content myself, therefore, with relating the results. From these it appears, that plants, when

* A full description of the natural phenomena of this interesting lake, is to be found in the "Last Days of a Philosopher," by the late Sir H. Davy.

† Priestley's Experiments and Observations on Air. Birmingham.

‡ Ingenhouz's Expériences sur les Végétaux. Paris.

|| Ellis on the Changes of Air, &c. Edinburgh.

moistened and exposed to a full sunshine, part with oxygen, and that the carbonic acid in the atmosphere is somewhat diminished, whilst in cloudy weather or in darkness, oxygen disappears, and is replaced by carbonic acid. It has been found also by the experiments of Saussure, that an atmosphere containing 8 or 9 per cent. of carbonic acid, was more favourable to the growth of vegetables than common air, provided the subjects of experiment were exposed to the sun ; otherwise the carbonic acid only proved prejudicial. That oxygen and carbon are both essential elements to vegetation, and that plants are capable of abstracting from the atmosphere either of these substances, is, I think, sufficiently demonstrable. If a plant be placed under circumstances where no carbon can be derived from the earth, (as in the experiment of Saussure, where a plant was kept in pure siliceous earth,) it will continue to grow and ripen its seeds, acquiring at the same time an increase of carbon, whilst the necessity of oxygen is sufficiently demonstrated by the very speedy decay of any plant when immersed in a gas which does not contain a large proportion of that element.* But if the influence of the atmosphere is essential to the growth and preservation of the adult vegetable, it is no less so to the development of the embryo in the process of germination. Here, however, it is the oxygen that is required, and accordingly we find that darkness is one of the essential conditions to the germination of seeds, because it is in darkness that an absorption of oxygen in vegetables appears most readily to take place. The chief chemical change that occurs during germination, is the conversion of the fæcula of the seed into sugar ; and as the oxygen absorbed for this purpose is replaced by an equal volume of carbonic acid, there is necessarily a loss of carbon experienced by the

* See Experiments by Turner and Christison, in the Edinburgh Journal of Science for January 1828.

embryo. Heat is likewise developed during the process, and probably as a consequence of it, so that the phenomenon bears a close analogy to the process of respiration in the warm-blooded classes of animals, but with this difference, that the chemical changes in the vegetable materials are more obvious than those experienced by the animal fluids. But the necessity of air for the germination and growth of the embryo, is a phenomenon by no means confined to the vegetable kingdom. Throughout every department of the animal world, the same necessity is obviously displayed. In oviparous animals, it is found that neither incubation nor artificial heat have any effect in the hatching of eggs, if the air be excluded from the outer surface of the shell. The prodigious journeys taken by fishes of the genus “*salmo*” to the sources of rivers, are well known. Their only object seems to be to deposit their ova in that part of the stream where the water is most abundantly impregnated with air. In viviparous animals, the embryo is receiving through the placenta the influence of the already aerated maternal blood; and any distinct process of aeration in the body of the fetus, appears not to be required. A similar disappearance of oxygen and disengagement of heat occurs in vegetables during flowering, and the sugar which is thus produced appears to be especially destined for the nourishment of the sexual organs, since it has been found by M. Dunal,* that these phenomena are in proportion to the development of the glandular disk, (as for example in the “*Arum dracunculus*,” which destroys in 24 hours thirteen times its volume of oxygen); and moreover, that they are most intensely active at the time when the anthers are most developed. Having so far detailed the reciprocal action of the elastic medium upon the “organic fluids” (or materials) of the living vegetable, I now proceed to describe, in as few words as possible, the

* *Dunal sur les Fonctions des Organes floraux, &c.* Paris, 1829.

"preliminary contrivances," employed by nature for this purpose.

Respiration in the adult phenogamic vegetable, is generally carried on through the medium of the leaves. These consist most commonly in broad flat expansions, varying, however, in form from orbicular to linear, sometimes simple, but frequently divided into segments of various depths. This diversity of form is easily accounted for, when we consider the structure of a leaf; it consists of ramifications of vascular fibres proceeding from the stem, having the interstices filled up with cellular tissue or parenchyma.* This filling up may be either entire, as in simple leaves, or partial, as in divided or compound leaves, thus giving rise to the difference of form which the leaf exhibits in different plants. The vascular fibres, having reached the extreme edge of the leaf or leaflet, turn upon themselves, and unite again on its under surface to re-enter the stem. In dicotyledonous plants the upper layer of fibres proceeds from the medullary sheath, the lower enters into the bark. It is to these organs that the sap or circulating fluid of the vegetable is conveyed, to part with a portion of its water, and to undergo the respiratory changes already explained. The sap thus changed, is returned to the bark, and is ready for nutrition. Other functions are performed by the leaves, but we are considering them only with a view to respiration; although the leaves are generally considered as the principal organs of respiration in vegetables, there is no doubt that other organs assist likewise in the process. The bractea, calyx and corolla, which are all mere modifications of the leaf, are also subservient to this important function, and in herbaceous vegetables which are said to be destitute

* For a minute anatomical description of this parenchyma, see Dutrochet's Memoir "sur les organes aerifères des Végétaux," in the 25th vol. of the "Annales des Sciences Naturelles," page 242.

of leaves, (as in salicornia) the round, fleshy and branched stems are no doubt fully adequate for this purpose.*

Of the Nervous System in Vegetables.

There is perhaps no subject in the whole range of vegetable and animal physiology, on which theories appear to have been more audaciously advanced, and less substantiated by proof, than the question of the existence of a nervous system in the vegetable kingdom. To me, indeed, it appears scarcely credible, that a doctrine which rests on such slender foundations, should have found among men of science many warm advocates and strenuous supporters. M. Dutrochet, for example, in his ingenious but speculative work, "Sur la Motilité," after describing certain microscopic globules in the interior of the cells of plants, which Mirbel had mistaken for communicating foramina, and shewing that their transparency in the centre had given rise to this error, observes, that by a drop of diluted nitric acid an opacity was produced, (an effect which bore some fancied resemblance to the action of this acid on the medullary or nervous matter of animals,) and leaning on this flimsy ar-

* That the condition of the atmosphere exerts an influence in modifying the form of plants, is a fact of which examples are not limited to the class "cryptogamia" alone. Professor Robison related in his lectures a circumstance which occurred to himself, illustrative of this influence, in a well known phenogamic plant. Having descended to the bottom of a coal mine, he found a weed growing in a tuft of grass, in a situation from which the light was excluded; on bringing it out of the mine and examining its leaves, he found them perfectly etiolated, and differing in form from any species hitherto described; deeming that he had made a discovery, he planted the specimen in the ground, in a situation freely exposed to light and air; he was not a little surprised, however, to find, that in the following spring, the supposed new species exhibited the leaves and flowers of the "common tansey," which he had not recognised when growing in its former situation. For this interesting anecdote, I am indebted to Dr Traill.

gument, he unhesitatingly jumps at the extraordinary conclusion, which he thus expresses, “ Je ne doute point que ‘ ce ne soit là le système nerveux chez les végétaux.’ ”

That plants, which possess only the power of self-preservation and reproduction as the manifestations of their vitality, and are totally destitute of those higher functions by which the animal kingdom is pre-eminently distinguished, should be considered as possessing a nervous system, appears to me in the highest degree preposterous and absurd. Destined by nature to remain fixed to the soil from which their nutriment is derived, organs of locomotion are in them, neither provided nor required ; hence one of the principal objects of a nervous system is entirely wanting, and the existence of nerves of locomotion may surely therefore be unequivocally denied, from the total absence of the ordinary phenomena which such a provision is found to produce.

The existence of sensation in the vegetable kingdom appears still more problematical than that of locomotion, for the idea of sensation necessarily involves the existence of a sensorium, and it is inconceivable in what manner this function can be assigned to vegetables, unless it be determined, in the liberal spirit of some philosophers, to bestow upon them the “ godlike attribute” of mind ; it is to be feared, however, that such a provision would only prove a source of perpetual disquietude, against which, their stationary condition would afford them no protection. On this point, it is surely needless to dwell : sensation without voluntary motion would be a function without an object, and it is not in this manner, that nature usually exhibits her powers of design in the construction of her creatures. As for the very few isolated instances in the vegetable kingdom, of phenomena supposed to indicate sensation and voluntary motion, as for example, the folding of the leaves of the “ *mimosa pudica*,” and the elastic spring of the anthers of the “ *kal-mia latifolia*,” I must confess, that there is nothing in these and other phenomena commonly mentioned, which has ever

appeared to me beyond the reach of explanation on physical principles, although the precise mode of explaining them may, as yet, be somewhat embarrassing. As for the phenomenon observed in the “*kalmia*,” it appears to be a simple instance of elasticity, which is possessed by the stamens of this plant in common with dead caoutchouc, and surely the action of the one and the other, might with equal propriety be ascribed to the influence of a nervous system. The phenomenon of the leaves of the “*mimosa*,” is, I confess, somewhat difficult of explanation ; I would venture, however, to suggest, that it is but a manifestation in a higher degree, of the property by which flowers unfold their petals to the sun, and close them again in the absence of its genial beams ; of the property by which they present the upper surface of their leaves to the heavens, and their radicles to the earth, all of which are probably dependent upon certain chemical or vital attractions existing between the constituent parts and the surrounding media,* and to ascribe them to the action of a nervous system, would be about as philosophical as to explain in a similar manner the attraction of the iron for the loadstone, or the rotation of the earth upon its axis. But it may be argued, admitting that,

* As a proof how much this is the case, it is only necessary to consult a very interesting memoir by Dutrochet himself, in the 25th vol. of the “*Annales des Sciences Naturelles*,” from which it appears, that if the “*mimosa*” be introduced under the exhausted receiver of an air-pump, its excitability is altogether suspended ; and so far is this from being explicable on the supposition that the plant is asphyxiated, and its vitality thereby destroyed, (as he endeavours to demonstrate,) that when the air is re-admitted, the excitability is promptly restored. It has been further shewn, by the same ingenious experimenter, that the phenomena of sleeping and waking exhibited by the petals of many plants, may likewise be effectually suspended in a similar manner. Even the solar beams were found to be absolutely powerless, if the atmosphere were artificially excluded. It really seems extraordinary, that with such proofs as his own experiments adduce of the real nature of these phenomena, he should still persist in considering them as manifestations of the agency of the nervous system.

the functions of locomotion and sensation being absent in vegetables, no nervous system exists for these purposes, may not the functions which do exist be of a nature to require nervous influence? To this I would reply with confidence in the negative. The circulation, for example, of the sap in the living vegetable, has been shewn by Dutrochet himself, to be explicable on physical principles; and the same principles are likewise applicable to explain the absorbing power exercised by the radicles. With regard to absorption in general, it may be here observed, that the error of ascribing this function to the influence of nervous agency, is sufficiently demonstrated by the fact, that fluids will transude through the tissue of a detached vein when applied to its outer surface, as beautifully demonstrated by Magendie; and if therefore this phenomenon can occur in a manner so obviously independent of the nervous system, even in animals where that system exists, it can scarcely be contended that the exercise of this function in vegetables, implies the necessity of any such co-operation or assistance. Neither can it be argued, that the process of assimilation in vegetables is any proof of the existence of a nervous system, for surely no one who reflects for a moment upon a process, by which, in the egg, the apparently homogeneous mass that constitutes the yolk is converted into all the wonderful structures of the adult animal, can entertain a doubt, that the process of assimilation to which the nervous system itself owes its existence, cannot be dependent upon any influence derived from that system.

I have dwelt at some length on this part of my subject, because it tends strongly to establish the conclusion, which I hope to demonstrate more fully hereafter, that the function of respiration, in itself considered, is not necessarily dependent on any nervous influence whatever, and that any apparent dependence in the higher classes of animals, has arisen merely from its connection with those "preliminary contrivances," to which, in the departments of nature al-

luded to, respiration is rendered subservient, in consequence of the more complicated structures which are there exhibited.

Respiration, as we have seen, then, can exist in one entire division of the organic world, in full perfection, and certainly in its full importance as an essential to vitality, under circumstances where the existence of a nervous system is altogether disproved, not only by the insufficiency of any direct evidence that can be adduced, but still more by the total absence of those phenomena, from which its existence might fairly have been inferred.

Of Respiration in Zoophytes.

The “essential” process of respiration in this, the lowest of the four grand classes of animals, is in all probability not different, except in degree, from that exhibited in the higher classes. But the “contrivances” for the exercise of this function are varied, and as yet, imperfectly understood. To the distinguished naturalist, Cuvier, we are chiefly indebted for the little that is known on this obscure but interesting subject. In the “infusoria,” he describes a toothed apparatus, to which a constant rotatory motion is communicated, and which he considers as subservient to this function.* In the “asterias,” respiration is accomplished by means of numerous tubes, with which the whole surface of the rays is abundantly furnished, and which appear to absorb water and convey it into the central or general cavity; with them, therefore, as in fishes, respiration is accomplished through

* This rotatory motion is suggested by Dutrochet, to be rather apparent than real, and to partake of the nature of a vibration, communicated rapidly round the circumference of the organ. The difficulty of reconciling this rotatory motion with any organic connection with the rest of the body, has led this philosopher to indulge in the foregoing ingenious speculation.

the medium of aerated water, while the tubular apparatus bears a close analogy with that of the insect tribe. In the “*ascidiæ*” the respiratory apparatus consists of a large cavity lined by a plicated membrane, and situated between the esophagus and external opening or mouth; in consequence of this distribution, the whole of the food passes through the respiratory cavity before it is transmitted to the stomach. In the “*holothuriæ*,” a very remarkable cavity of an arborescent form (*arbrecieux*) communicates with the rectum, and may be filled or emptied of water at the pleasure of the animal. In the “*intestinales*” alone do we find no vestiges of respiratory apparatus, that function, as in the “*foetus in utero*,” being probably performed for them by the animals, in the interior of whose cavities they are destined to dwell. In animals of the “*medusa*” kind, but little apparatus is required for the function of respiration; for the gelatinous consistence of their whole bodies, and the abundant vesicles with which they are furnished, render the contact sufficiently intimate for those changes which, from analogy, we must suppose to occur between the fluids of which they consist, and the constituents of the atmosphere.*

Of the Nervous System in Zoophytes.

The indefatigable Ehrenberg has succeeded in discovering some traces of a nervous system in a few of the larger species of “*infusoria*,” an order of zoophytes in which there appear to be the most obvious demonstrations of volition. In the medusa tribe, on the contrary, in which

* The four lateral cavities in the “*medusa pulmo*,” which are contiguous to the great central receptacle or stomach, but separated from it by membranous septa, have by some been considered as organs of respiration. This, however, is an hypothesis which rests altogether upon conjecture.

the manifestations both of volition and sensibility are very obscure, nothing bearing the least resemblance to nervous matter has hitherto been discovered. The existence of a nervous system in “sponges” is rendered improbable by what has been said when speaking of the vegetable kingdom, from which indeed they seem to be distinguished, not by any superiority in their sensitive or locomotive* functions, but simply by their receiving from an internal cavity the materials to be assimilated, which, in vegetables, are derived directly from the soil or the atmosphere.

Of Respiration in the “Articulata.”

The “contrivances” employed for respiration in this and the two following classes, admit of a twofold division ; one according as the elastic fluid is conveyed to the animal in its elastic state, or in solution in water ; the other, according as the fluid of the animal is brought into contact with the air, by means of a vascular apparatus, or the air brought to the fluid by means of tubes or tracheæ.

In the class we are now considering, all these varieties are exhibited. In the “annelides” we find animals provided with red blood and a double system of arteries and veins, but respiring by gills of a “plumose” or “arborescent” form ; while others, as the earth-worm and leech, are provided with a separate respiratory cavity or vesicle between each of their annular segments, into every one of which the water is received by a corresponding external aperture. The number of these vesicles varies in different

* Since writing the above, I have read some interesting observations by Dr Roget, in his Bridgewater Treatise, from which it would appear that young sponges, when first detached from the parent, possess a locomotive power for a short period, until they have chosen a point of attachment, where they remain for the rest of their existence.

families. Others, as the "aphrodita aculeata," have but one large respiratory cavity, with which the external openings are all found communicating. In the class "crustacea," respiration is always branchial. The gills are attached generally to some part of their articulated feet, their form and situation varying respectively in every order of the class, as in the crab, wood-louse, monocus, &c. The circulation is double, with a great dorsal vessel, and a true branchial ventricle. In the "arachnidæ," respiration may be either pulmonary or tracheal, and this has given rise to two grand orders, into which this class has been divided. In both orders, the stigmata or breathing holes are placed beneath the abdomen, but in the one they terminate in saccular organs, with the parietes of which a laminated* respiratory apparatus is connected, and to which the blood is conveyed by a dorsal vessel; in the other, the stigmata terminate in "tracheæ," or air-tubes, which send ramifications to all parts of the body. Spiders, scorpions, &c. are examples of pulmonary arachnidæ. The animals called false scorpions, furnish an example of those whose respiration is tracheal. The "insecta" breathe universally by tracheæ. They are furnished with a large dorsal vessel, extending the whole length of the body, through which the blood flows uniformly in one direction. This fact, for which we are indebted to the investigations of Professor Carus, is at length established beyond the possibility of a doubt. From these researches it appears, that the streams of blood which permeate the body of the insect, enter the dorsal vessel at the posterior extremity, and pass out of it anteriorly. The existence of valves in this vessel tends to corroborate still further the truth of this assertion. The insect tribe presents us with a

* It is the laminated structure of the lining membrane of these pulmonary cavities which has procured for them the very inappropriate appellation of "Pneumobranchia."

beautiful illustration of the diffused and vascular circulations co-existing in the same individual. These circulating streams become less visible as the insect passes from the state of larva to that of imago, at which latter period the dorsal vessel is almost the only visible agent in the circulation. The “tracheæ” consist of two principal trunks, parallel to each other, extending longitudinally through the body, and furnished with centres, from which numerous ramifications proceed, and which correspond to the stigmata or external openings on the surface, through which the air enters in its elastic state, and circulates, as it were, through the body of the insect.* This mode of respiration is uniform throughout every order of this numerous class of animals.

Of the Nervous System of “Articulata.”

We are now arrived at that division of the scale of organization in which a nervous system is uniformly discovered to exist. Its appearance is but little diversified in the different orders of the class, and is thus described by Cuvier. “The brain is situated upon the esophagus, and furnishes nerves to those parts connected with the head; it is very small, two nervous cords proceeding from it, surround the esophagus, and are continued throughout the whole length of the abdomen, uniting at different intervals into double knots or ganglia, from which nerves are found proceeding to the trunk and limbs.”† In pursuing the comparative investigation of these ganglia, as we ascend from the lower to the more perfect animals, we find uni-

* The middle coat of these tracheæ consists of a cylindrical spiral thread, (like the air-tubes in the vegetable kingdom,) by the elasticity of which they are kept permanently open.

† *Regne Animal*, tom. 2.

formly a tendency to coalesce into fewer centres. This disposition to progressive concentration of nervous power, is particularly exhibited in insects, where it observes a regular gradation corresponding to their different degrees of development. Accordingly, it is found that the ganglia are more numerous in the larva than in the chrysalis, where a considerable aggregation is exhibited, which is still more obvious in the imago, or perfect insect. In addition to the nerves above described, another distinct series of ganglia or plexuses, situated transversely in relation to the former, has been described by Mr Newport, in the sphinx ligustri.* The distribution of some of the nerves arising from these ganglia, to the larger branches of the tracheæ, has led their discoverer to conjecture that this system is designed exclusively for respiration. It is remarkable, however, that the nerve supposed to correspond to the pneumo-gastric, does not originate from any of these plexuses, but from the cerebral ganglion of the principal series. If the series of ganglia first described, are to be considered as analogous to the cerebro-spinal axis, it appears to me more probable that this second series may correspond to the sympathetic system of vertebrate animals.

On Respiration in the “Mollusca.”

Animals of this class are all provided with a double circulation of white blood. They breathe the air in its elastic state, or in solution in water, according as they are terrestrial or aquatic. In the “mollusca cephalopoda,” the respiration is branchial. The gills are, in form, like a compound fern leaf; the vena cava divides into two, and each branch discharges its blood into a fleshy ventricle for

* Phil. Trans. 1832.

each of the gills ; a third, or aortic ventricle, receives the returning blood from both gills, and propels it through the body. Such is respiration in the *sepia* and *nautilus*. In the “*mollusca pteropoda*,” the gills are situated externally on each side of the neck, serving the double purpose of progressive motion and respiration. The “*clio borealis*” of the northern ocean, furnishes the best example of this peculiar distribution of the gills. In the numerous animals belonging to the “*mollusca gasteropoda*,” the respiratory organs are always in the last spire of the shell ; the form and attachment of the gills have given rise to the method of subdivision employed by Cuvier. Accordingly, we find them divided into “*nudibranchia*,” “*pectinibranchia*,” “*tectibranchia*,” and “*cyclobranchia*.” In one order only do we find the air respired in its elastic state, from which circumstance they have received their appellation of “*pulmonary gasteropoda*.” They are provided with a large respiratory sac, over which a net-work of blood-vessels is seen ramifying in all directions, the aperture into which is defended by a sphincter muscle ; we have as yet no approach to the cellular structure of the lungs of the higher terrestrial animals. The snail and slug are examples of *mollusca* of this description. In “*mollusca acephala*,” the gills are leafy expansions covered with a vascular net-work, between which the water is received. They are particularly distinguished from the other “*mollusca*,” in having a single ventricle which is aortal, there being none provided to propel the blood into the gills. The oyster is a familiar example.*

* The manner in which this animal provides for its respiration during the retreat of the tide, was first noticed by Diquemare ;* it consists simply in closing the valves of the shell, and thus retaining between them a sufficient quantity of water to serve for respiration, until the return of the tide. Those oysters which were taken from greater depths were observed speedily to perish when removed from the water, from neglect of this precaution.

* *Journal de Physique*, Tom. xxviii. p. 244.

Of the Nervous System in the “Mollusca.”

The nervous system in this class bears a close resemblance to that in the preceding ; there is no union of the nervous cords into a spinal marrow, but only into medullary masses or ganglia, which exhibit a greater tendency to the circular than the longitudinal arrangement in relation to each other. The largest of these encircle the esophagus.

Of the real function of Respiration in the two preceding Classes.

Experiments on the changes produced in the atmospheric air by the respiration of invertebrate animals, were conducted with great care by that indefatigable physiologist Spallanzani,* and some of them have been recently repeated by Dr Edwards.† The result is, to prove that the changes are closely analogous, if not identical with those produced by the respiration of the vertebrate animals ; that although, like many of the “batracia,” they can endure an atmosphere devoid of oxygen for some hours, yet that a longer period of privation proves fatal to their existence ; that the air respired contains carbonic acid, and that when immersed in hydrogen or other gases destitute of oxygen, carbonic acid is nevertheless produced during the experiment. Of those which respire aerated water, the capacity of enduring the deprivation of oxygen is increased or diminished inversely as the temperature.

Of Respiration in Fishes.

In this class of vertebrate animals, respiration is univer-

* Mem. sur la Respiration. Geneve 1803.

† Influence des Agens Phys. sur la Vie.

sally accomplished through the medium of water. That this fluid is the only medium through which fishes can receive air for any lengthened period, is sufficiently proved by exposing a fish for a few minutes to respiration in the atmosphere. The real cause of a fish's inability to continue its existence by means of atmospheric respiration, has long embarrassed the naturalist and the physiologist. To Dr Edwards and his ingenious experiments we are indebted for the best explanation of this curious fact. That fishes can breathe air in its elastic state, and that by doing so occasionally their existence in water is prolonged, was proved by the experiment of Sylvestre, who found that if a diaphragm were placed over the surface of water in which a fish had been immersed, death occurred much sooner than when free access to the atmosphere was permitted. It is therefore obvious that the death of fishes in the atmosphere is not attributable to any unfitness in the condition of that fluid for producing the necessary changes upon the fluids of the animal, (as was long supposed,) although until the experiments of Dr Edwards had contributed to throw light upon the subject, there appeared to be no other mode of explaining the phenomenon. It is now, however, clearly demonstrated, that a fish when removed from the water, loses by evaporation from the surface of the skin a quantity of fluid amounting to $1\text{-}14^{\text{th}}$ of its weight, and that this loss is quite sufficient to paralyze the muscles of the gills, and thereby render further respiration impracticable. That it is not death by inanition which is thus produced, is further proved by immersing the tail of the fish in water, and keeping it for some time in this situation, the head and apertures to the gills being exposed to the air. In this position, the fish will actually gain in weight from the absorption carried on in the tail, but the gills will beat languidly for a time, and then entirely cease their pulsation. If the gills are elevated by a peg so as to be kept exposed, respiration may be continued for some time longer; if the

experiment be reversed, and the tail only of the fish be removed from the water, the head and gills remaining immersed, the fish continues to live and to increase in weight, but the tail becomes dry on the surface, shewing that the fluid thus absorbed was not distributed to the tail in a proportion sufficient to repair the loss sustained by perspiration in air.* The respiration of fishes when removed from aerated into non-aerated water, is influenced in a remarkable degree by the temperature of the medium. A fish immersed in water, deprived of air at 32° , will live much longer than the same fish immersed in the same fluid at 104° . Scarcely any fish will live more than two minutes in water of 104° deprived of air. The period to which life may be prolonged in non-aerated water at low temperatures, varies with the species. The same effect of temperature is observed in a limited quantity of aerated water.†

The respiratory apparatus in fishes consists of thin leaflets or laminæ, over which innumerable vessels are distributed, and which are attached to arches connected with the os hyoides. The water is swallowed by the fish, and escapes between these laminæ by apertures for that purpose. The blood is propelled into the gills by a fleshy heart, which represents the right auricle and ventricle of warm-blooded animals. Cartilaginous fishes have, many of them, the gills fixed on the outer edge, and present as many external apertures for the escape of the water as there are interspaces between them. The lamprey, the ray, and the shark, have

* A somewhat different explanation of these phenomena as exhibited in fishes, has been attempted by Flourens; he endeavours to ascribe the cessation of the action of the gills, to the loss of the momentum of the water, in unfolding and expanding the branchial filaments, rather than to any loss of power in the muscles occasioned by their exsiccation.

† The smallest quantity of oxygen which has been known to support the life of a fish for any considerable period, is 1-5000th of the bulk of the fluid; the usual average in river water is one per cent.—*Edwards.*

their respiratory organs thus constructed.* Others have but two openings beneath the abdomen, and are called "gastrobranchia." The sturgeon, on the contrary, has the gills unattached by the outer edge, and but one common external aperture. Of the osseous fishes, the chief deviation from the ordinary disposition of the gills, is in the curious order "lophobranchia," where the gills, instead of being, as usual, like the teeth of a comb, are disposed in circles on each side of the branchial arches. They have but one small external aperture. The pipe-fish presents an example of this structure. In the "perca scandens," there exists in the pharyngeal bones a peculiar contrivance, by means of which the air is retained for a sufficient time to supply the demands of the animal while travelling to a distance on land.

Of the Nervous System in Fishes.

We are now arrived at that division in the scale of organization, in which we have the first appearance of a cerebro-spinal system of nerves. The nerves of fishes are united into a spinal chord, which, as in the succeeding classes, is enclosed in a vertebral canal, and is divisible into anterior, middle, and posterior pillars, each of which terminates respectively in symmetrical lobes within the cranium. In fishes the anterior lobes are comparatively little developed, appearing to be chiefly connected with the sense of smell, and are called the olfactory tubercles. The middle or optic tubercles are considerably developed, being

* The design of nature in thus providing these animals with so many external apertures destitute of operculum, seems to be, to render their respiration independent of the mouth, in order that this function may not be impeded whilst they are engaged in seizing and devouring their prey.—*Roget's Bridgewater Treatise.*

much larger than in mammalia and birds ; but the lobes which are least developed in fishes, are those of the cerebellum. As in fishes, the organs of respiration are situated within the head, there is no diaphragm required, neither are there any ribs properly so called, those which are so denominated having no connection with respiration, and being of the nature of floating ribs, or probably mere vestiges. The phrenic nerve is of course entirely wanting, and the nerves corresponding to intercostal, have no connection with respiration. In fact, the "preliminary condition" for this function in fishes is an act of deglutition, for which the glosso-pharyngeal and ninth nerves are chiefly instrumental. We find accordingly, that no injury of the spinal chord is destructive to this function in fishes. In animals in which the mechanism of respiration differs so widely from that of the other vertebrata, as it does in fishes, it is not surprising that we should find other nerves subservient to this purpose ; and this tends only to establish the position, that the influence of the nerves is not upon the function of respiration itself, but merely upon the mechanical contrivances which nature has recourse to, in animals of complex organization, to promote the contact of their fluids with the oxygen of the atmosphere.

Of Respiration in "Amphibia."

The phenomena connected with the respiration of this class of animals are so extraordinary, and many of them so totally at variance with those observed in any other department, that they would scarcely be credited, were they not authenticated by very numerous facts, and established by repeated experiments. In frogs and other batracia, for example, such is the tenacity of life which is displayed, and so numerous are the methods by which respiration is accomplished, that they will continue to live for many days,

when the lungs have been completely removed by excision,* or the air excluded from them by strangulation ;† respiration all the time through the medium of the skin. When immersed in aerated water, the duration of their existence depends in a great degree, as in fishes, upon the temperature of that medium.‡ At 32° Fahr. they will exist for a long period in water of which the air is unchanged ; but if the elevation of the temperature equal or exceed 56° Fahr., and they are excluded from atmospheric respiration, they speedily die, although the water in which they are immersed, may be changed with the greatest rapidity. It is remarkable, however, that when thus retained under aerated water, although, by lowering the temperature, their existence is prolonged, they lose their activity, and become remarkably sluggish and torpid. But the most wonderful phenomenon connected with batrachian respiration, is the endurance of life which they exhibit, when incarcerated for years in solid materials, as marble, mill-stone,|| grit, &c. of which several instances are on record. That the quantity of air necessary for supporting existence in this state of torpor is extremely small, is the only method of accounting for this curious phenomenon ; but it is further proved, by experiments of Dr Edwards,§ that the reason that frogs live longer when inclosed in solid bodies, than in air, is to be sought for in the greatly diminished loss by perspiration in the former media. That they do actually respire, when thus incarcerated, in a degree sufficient to support life for a long period, under the favourable circumstances of inaction and diminished evaporation, is, I think, satisfactorily proved, by enclosing animals in plas-

* Edwards, Influence des Ag. Phys. sur la Vie. † Id. ‡ Id.

|| A case of this kind (communicated by a surgeon from Brough in Westmoreland) was related by Dr Blundell, together with several others, in his Lectures on Physiology.

§ Infl. des Ag. Phys. sur la Vie.

ter, and after allowing it to consolidate, plunging it into water or mercury, so as to intercept the external air. The animals die as rapidly after the immersion of the plaster, as when they are themselves immersed and retained in water ;* hence it is evident, that the air which penetrates the plaster, is sufficient to preserve life under the circumstances already explained, since its exclusion proves rapidly fatal to their existence.

Of the Influence of Respiration on the Form of Batracia.

The influence of the atmosphere on the form of organized structures, has been already noticed in another part of this dissertation ; but in no class is this influence more strikingly exhibited, than in that of the batracia. It was ascertained by Dr Edwards, that a tadpole's metamorphosis may be entirely arrested by constant immersion in running water, provided nutriment be not too abundantly supplied, and the temperature be not too high. The exclusion of light is also necessary for the success of the experiment. Out of twelve tadpoles which he kept immersed, two only underwent the natural metamorphosis, the other remained unchanged till death.†

I cannot conclude the subject of amphibious respiration, without adverting to that very extraordinary and interesting animal lately discovered in the subterranean lakes of Carniola, in Illyria. I mean “the Proteus.” This animal is provided with a double respiratory apparatus, by which it is enabled to exist either above or below the sur-

* Dr Edwards, Ib.

† For some further illustrations of the influence of light upon the metamorphosis of frogs, I am indebted to some experiments performed by Dr Inglis, and related by him, in a communication read before the Royal Medical Society, January 2, 1835.

face of the water. Its lungs are like those of the rest of the lizard tribe; but besides these, it is provided with a crested vascular apparatus of branchiæ, which surround the throat, and which may be removed without destroying the life of the animal. I believe the "proteus" is the only instance that has yet been discovered, of the pulmonary and branchial respiration co-existing throughout life in the same individual.

Of the Mechanism of Respiration in "Amphibia."

As frogs are quite destitute of ribs, the air which enters the lungs is introduced by an act of deglutition; accordingly, if the mouth of a frog be kept forcibly open, pulmonary respiration is almost entirely arrested. In tortoises, the ribs are so closely united, to form the bony covering of the shell, that any motion between them is impossible. In inspiration, the jaws being first firmly fixed, the os hyoides is elevated, and the air enters through the nostrils; the tongue is then placed over the nasal aperture internally, and the os hyoides depressed; by this means, the air is forced into the lungs. Expiration is performed by the muscles of the abdomen. The lungs, in the tortoise, are of large size, and extend into the cavity of the abdomen, separated, however, from the other viscera, by a reflexion of peritoneum. In lizards and serpents, a more perfect apparatus is provided. In the former tribe, the ribs are moveable, and attached to a sternum. In the latter, they are unattached, but form the greater part of the circumference of the trunk, being designed for progressive motion, as well as respiration. In none of the class "amphibia," do we find any vestige of a diaphragm, except in the crocodile; in this animal, a few fleshy fibres attached to the peritoneal surface of the liver, present a kind of approxi-

mation to this muscle. In them, also, the lungs do not protrude into the abdomen, as in the other "amphibia."

Of the Nervous System of "Amphibia."

In this class, we find the whole of the cerebral mass bears a small proportion to the rest of the body, and there is scarcely a vestige of cerebellum. Their sensations appear to be very obtuse; their movements consequently slow. In them, therefore, muscular irritability is slowly expended, and will continue for some time after decapitation. The heart, in particular, is found to be remarkably tenacious of its contractile power, as proved by the length of time during which it continues to palpitate when excised. The phrenic nerve is, of course, wanting; and the principal nerves connected with respiration, are those distributed to the larynx, pharynx, and os hyoides.

Of Respiration in Birds.

If the class we have just been considering, appear to exhibit, as a distinguishing characteristic, a tenacity of existence not found in other vertebrata, and a less frequent necessity for a renewal of the oxygen of the atmosphere to support respiration, the converse is no less remarkable in the animals which now claim our attention. Here we behold the phenomena of life displayed, as it were, in their fullest activity; whether we regard the perfection and rapidity of their muscular movements, the elevated temperature of their bodies, their highly animalized vital fluid, or the extensive development of their vocal and respiratory organs, we must still feel disposed to consider them as peculiarly fitted, by their structure and functions, for the highest state of physical enjoyment. In other animals, as

we have seen, the atmosphere appears to be simply a medium for the purification of the vital fluid. To birds, it is, as it were, a native element; by the peculiar internal conformation of their bodies, it is enabled to permeate every texture of their frame; and whilst it thus imparts to every nerve and fibre the most lively sensations, and the most active irritability,* it enables them, by the diminished specific gravity of their bodies, when,

“ ————— Tir'd of earth,
“ And this diurnal scene, to shoot aloft
“ Through fields of air; pursue the flying storm,
“ Ride on the volley'd lightning through the heavens,
“ And yok'd with whirlwinds and the northern blast,
“ Sweep the long tract of day.”

It is therefore no longer surprising that animals, in whom the vital energies are so actively developed, should require a very rapid and abundant supply of oxygen, to animalize, as much as possible, the vital fluid. Accordingly, we find that the same quantity of air which would support the life of a frog during three or four days, will maintain a bird, though one of the smallest of the tribe, only for a single hour. The average number of respirations is from 80 to 100 in a minute, which is four or five times greater than in man: the blood is likewise found to contain about double the quantity of “ fibrine,” amounting, in the common fowl, to 8 parts in 1000, whilst the number and dimensions of the red particles (according to Prevot and Dumas) differ materially from those of other animals. In short, their blood contains much more of the

* By the term “ irritability,” it is here intended to express activity of contractile power, and not its tenacity. It is this latter property, however, to which Dr Marshall Hall refers, when he attempts to establish that respiration and irritability are inversely as each other.—See a Paper in Phil. Trans. for 1832, page 321, et seqq.

solid, and less of the watery particles. Birds are likewise enabled, by the great perfection of their respiratory apparatus, to maintain the temperature of their bodies under a great reduction of the warmth of the external air. In order to accomplish this, their respiratory movements are much accelerated, amounting in some experiments to 120 in a minute.*

But if the vital energies are more active, the tenacity of life is very far inferior to that of reptiles and fishes. Birds are (with some exceptions) generally short-lived, and in them any check to their natural functions proves rapidly fatal. Even their endurance of cold is very limited, and in a vitiated atmosphere, as already stated, they very speedily die. Hence we find, that nature has distributed her advantages more equally than would at first appear. The seemingly inferior degree of enjoyment, experienced by reptiles and fishes, is compensated by the greater length to which their existence is commonly prolonged; whilst the pleasures of the aerial choristers, however exquisite in kind, are fleeting and transient in duration.

Of the Mechanism of Respiration in Birds.

The most striking characteristic by which the respiratory apparatus in birds is distinguished from that of other vertebrata, whose respiration is pulmonary, consists in the passage which it affords for the penetration of the elastic fluid, not only among the ramifications of the pulmonary artery, but likewise among those of the aorta, in all parts of the body. For this purpose, the lungs are not, as in the other classes, unattached to the parietes of the chest, but fixed firmly to the ribs, and covered by a membrane full of apertures, through which the air is transmitted into

* Edwards, *Infl. des Ag. Phys.*

the cavity of the abdomen, and likewise into the extremities of the body, penetrating into the interior of the bones themselves. By these contrivances, a more complete arterialization is accomplished, than in any other animals whatever; and it is probably to this circumstance that the great activity of their muscular movements is mainly to be attributed. It may, perhaps, be not undeserving of notice, that a similar diffusion of air throughout the body is provided in the class "insecta," already considered, although their apparatus for that purpose is altogether different. In them, a similar degree of irritability is likewise exhibited, and as in birds, the period of their perfect existence is of short duration.

Of the Nervous System in Birds.

On this subject a very few words will suffice. The nervous system in these animals is distinguished from that of the preceding classes chiefly by the difference in the proportions of its several parts. In birds, the encephalon bears a much larger proportion to the remainder of the cerebro-spinal axis. There is less development in the "corpora quadrigemina," or "optic tubercles." The cerebellum is of moderate dimensions, but the hemispheres are very thin, and destitute of convolutions. The nerves connected with the respiratory function are the same as in the class "mammalia," the phrenic alone excepted, which, together with the diaphragm, is altogether wanting in these animals.

Of the Mechanism of Respiration in Mammalia and in Man.

The same distinction which exists between vegetables and animals with regard to the function of digestion, ap-

pears to exist between some of the inferior classes and that which we are now considering, in relation to respiration. For as animals are impelled by the sensation of hunger to search for food, and to introduce it into the digestive cavity by a voluntary act ; in like manner the order we are now considering, and probably all the vertebrata, are warned by a sensation of uneasiness, which if unattended to soon becomes intolerable, to seek for a renewal of the air, and are provided with a muscular apparatus subjected to the will, for the accomplishment of this purpose. So imperative, indeed, is this necessity, that even in sleep, when all other efforts of the will appear to be at rest, the mind is still directed to this object, as may be easily proved by impeding the free access of air to an individual when asleep, and observing the deep inspiration which will immediately follow. The effect of profound and anxious thought is another illustration of the real nature of the respiratory movements, for when, by the influence of intense feeling, the mind is distracted from objects of habitual attention, respiration for a short interval is nearly suspended, and the uneasiness which speedily follows can only be relieved by a sigh, or (to substitute the physiological for the sentimental phraseology,) by a long-drawn full inspiration.

The will being thus powerfully called upon to act, various muscles are in readiness to obey its dictates. In ordinary respiration, where no unusual effort is required, the diaphragm alone suffices for inspiration, by changing from the convex to the flattened or concave form, and thereby enlarging the capacity of the thorax from above to below. This object being achieved, atmospheric pressure accomplishes the rest, and the air rushes into the cells of the already expanded lungs. In more forced inspiration the chest is raised, and the sternum brought forward by the action of the intercostal muscles which elevate the ribs, and at the same time widen their intervening spaces. The lateral parietes of the chest are held apart by the “*serratus magnus*,”

the scapula being fixed. This muscle (according to Sir Charles Bell,) is designed to serve the part of an antagonist to the diaphragm, by counteracting its tendency to approximate the lateral parietes, which would have the effect of diminishing the capacity of the thorax in one direction, while it increased it in another. In the more violent inspirations, other muscles, as the "sterno-cleido-mastoidei," and "trapezei," with the "pectorales minores," assist in raising the ribs. Expiration, when simple, is accomplished by the resiliency of the lungs and the relaxation of the diaphragm, aided by the elasticity of the cartilages of the ribs, and the weight of the abdominal viscera. In forced expiration, the abdominal muscles forcibly depress the ribs, and in the more violent expiration, as in sneezing or coughing, the numerous and powerful muscles of the back are all called into action in obedience to the will, to remove the irritation from the air-passages. Besides these there are other muscles, as those of the glottis, which are subsidiary to respiration, and are designed to modify the capacity of the air-passages, all of which are likewise in strict obedience to the will. We see, then, that in these animals, respiration, like digestion, although a function in itself, independent of nervous influence, is so situated with regard to its preliminary conditions, that it can only be exercised in obedience to the will as communicated through the nerves; and consequently, that respiration, although originally an independent function, has been rendered in man and mammalia incidentally dependent upon nervous influence.

*Of the Real Function of Respiration in Mammalia
and Man.*

It would be an unreasonable encroachment upon the time and patience of the reader, to relate the wild and extravagant speculations which were formerly indulged in by indi-

viduals otherwise much distinguished as physiologists, and which, previously to the discoveries of Priestley and Lavoisier, had many of them illustrious votaries, with a view of explaining the influence of the atmosphere on the blood of these animals. “Aer sanguinem refrigerat,” says Aristotle; and the opinion of this illustrious philosopher of antiquity was long after adopted by physiologists of more recent times, who added sundry explanatory speculations of their own. Aretœus has likewise transmitted to us the following pithy sentence on the subject,* “Cor sanguinem exurit, ita “in pulmone facit desiderium aeris frigidi.” In conformity with this theory, most of the older physiologists believed that the air existed in the blood-vessels in its elastic state; an opinion which is gravely confuted by Boerhaave. Even the celebrated Haller has strangely misunderstood this function, and ascribes to the air no further influence than merely, by expanding the lungs, to allow of the transmission of the blood more easily through them, in which case, it would surely have been better to dispense with the pulmonary apparatus altogether. He says,† “Respiratio “adeo vis est accessoria, quæ sanguinem abdominis quatit, “subigit, ex suis visceribus expedit, et cordi celeriter re-“mittit.” These and similar speculations are now become mere matters of history, interesting however, as shewing how uncertain are the most established dogmata of science, although resting upon the authority of men the most enlightened of their age.

The phenomena of respiration, since the discovery of Lavoisier,‡ have assumed altogether a different appearance, and so completely have opinions been changed, that the blood, instead of being cooled by the air, is now generally admitted to be warmed by that fluid. But although the main

* *De Causis Morborum*, fol. 1735. † *Elementa Physiologiæ*, tom. iii.

‡ *Essay on Atmospheric Air*, 1783.

phenomena, as far at least as the changes in the atmosphere are concerned, are now universally admitted and understood, physiologists are still divided in their views relative to the situation in which these changes take place; one party holding with Lavoisier, that they occur in the lungs, the other with Dr Edwards, that it is in the extreme capillaries of the body that these changes are effected. As I do not intend to enter at length into this discussion, I shall content myself with briefly stating the reasons which induce me to believe, that the latter physiologist's opinions on this subject are erroneous. In the first place, if, as he contends, the oxygen be absorbed at the lungs and enter into the blood, whence is it that arterial blood is not found to contain more oxygen than venous?* What becomes of all this gas in its passage from the lungs to the capillaries? In the next place, if the dark colour of venous blood be attributable, not to the presence of free carbon, but of carbonic acid, whence is it that caustic alkalies, (lime water in particular,) do not restore the arterial colour by neutralizing the acid? The reverse, however, is the fact. No change takes place by the agitation of venous blood in lime water, as particularly stated by Dr Stevens, and verified by myself; while the fact of acids darkening the colour of the blood, is surely a proof that this dark colour is given by the deposition of carbon, since we know that acids, when acting upon animal substances, have a strong tendency to leave a deposit of carbon, from their affinity for two other elements

* The only chemist who pretends to have discovered oxygen in an uncombined state in arterial blood, is Girtanner. (Adclon's Physiologie, vol. iii.) The blood employed was that of the sheep, which he kept under a receiver of azote for some hours, until a candle introduced under it was *not* immediately extinguished. His experiment, however, has been repeatedly tried by others, and never with the same results. Dr Edwards does not even mention it, and is himself evidently quite at a loss to determine, what becomes of the oxygen in the circulation. Query Might not the oxygen resulting in Girtanner's experiment, be simply the product of putrefaction?

of those textures. In the third place, the appearance of carbonic acid, when animals are immersed in a gas devoid of oxygen, is not a sufficient proof that in ordinary circumstances carbonic acid is excreted from the body independently of oxygen ; for it must be remembered, that the intestinal canal and the air already in the lungs are obvious sources of carbonic acid, and although these may in some instances be insufficient to supply the quantity produced, there is still another source of fallacy which Dr Edwards has entirely overlooked in his conclusions, namely, the quantity of gas which may have been absorbed and retained by the carbon of the animal body, in pursuance of a well known property of that substance, of absorbing gases which may subsequently be given out, when the animal is placed under the circumstances alluded to. Lastly, but little confidence can, I think, be placed in the slight disproportion alleged to exist between the oxygen of the inspired and the carbonic acid of the expired air, the rather, that other very accurate experimenters* have found them to correspond exactly; and at all events, their near approach to correspondence is a very strong argument for the dependence of the one upon the other, not through the medium of absorption and exhalation, but of direct chemical action of the one element upon the other when brought into contact in the lungs.

In thus stating what appears to me the objections to the opinion advanced by Dr Edwards, I do not by any means wish to intimate, that the lungs ought to be considered as mere passive organs in respiration. I am not now speaking of inspiration and expiration, or the part taken by the lungs or bronchial tubes in the mechanism of these processes. This question I leave to be decided by Reisseissen† and his followers ; but with regard to the respiratory changes

* See a paper by Messrs. Allen and Pepys in the Philosophical Trans. of London, 1808.

† *De Fabricâ Pulmonum Commentatio*, fol, 1822.

themselves, I do not wish, in representing them as purely chemical, to deny that the lungs exercise a powerful absorbing and exhaling influence through the membrane that lines them. This I conceive to be necessary to respiration, whichever view of that function be adopted, for without it, there could not be that close approximation of the elements which is necessary to chemical union. I need only refer to Dr Williams's experiments* for a full proof of the permeability of membranes to gaseous bodies, or to those of Dr Stevens† on the same subject; although the inferences which these experimenters deduce from their observations, by no means necessarily follow; nor is the truth of Dr Edwards' opinion in the least established, by this permeability being admitted.

After all the remarks which have preceded, the reader will easily have anticipated that I am not an advocate for the opinions of those physiologists, who consider that the real function of respiration in man and mammalia is dependent upon an influence derived from the eighth pair of nerves. Omitting for a moment all reasoning from analogy, and confining our attention exclusively to respiration as it occurs in these animals, we shall soon find that the evidence intended to be adduced from experiment in favour of this position, is wholly unsatisfactory. The principal physiologist who appears to have performed direct experiments, with a view of establishing this position, is M. Dupuytren.‡ The horse and the dog were the animals which he made the subjects of experiment. He informs us, that when he had cut through the eighth pair and great sympathetic on both sides in these animals, he opened the facial artery, and found that the blood flowed out of it of a dark colour. All the arteries of the body, he further observes, contained

* Med. Chir. Trans. of Edinburgh, vol. ii.

† Stevens on the Blood.

‡ Adelon's Physiology, vol. iii.

blood of the same colour, but this blood, though darker than arterial, was not so dark as venous blood, but intermediate in colour between the one and the other. He likewise ascertained, that when, instead of cutting, he only compressed these nerves, a similar change of colour appeared in the blood while the compression continued, but that it resumed its natural hue when the pressure was removed. It was further remarked, that after the section of these nerves death did not occur immediately, but after ten hours when the experiment was tried on horses, and not until the expiration of two or three days when it was repeated on dogs. To all this, the following objections unavoidably present themselves. If the arterialization of the blood depended upon the influence of the eighth pair of nerves, can it for a moment be supposed, that when that influence was cut off, and the animals reduced therefore to a state of complete asphyxia, they could survive ten hours, or even as many minutes in this condition? It must be remembered that these were not batracians, but dogs and horses upon which he operated, animals that require renewal of arterialization as frequently as man himself. But it is admitted by M. Dupuytren, that the stoppage of arterialization was not sudden, but gradual and partial only; and to explain this obvious inconsistency, he is obliged to have recourse to the expedient of assuming that the influence of the nerve continues for some hours after it has been divided. But is not this contrary to all that is known of the phenomena of nervous influence? Do we find that motion and sensation continue when the nerves subservient to these functions are separated from connection from their centres? Of what nature then is this extraordinary influence, which can continue for hours and days after the nerve which conveys it has been divided? Such an hypothesis has more in it of subterfuge than of reason. Add to which, M. Blainville has repeated M. Dupuytren's experiments, and found no such change in the colour of the blood as he describes; it

is moreover notorious to every student of physiology, that after an animal had been decapitated, Mr Brodie* first, and Mr Hastings† afterwards, carried on the arterialization of the blood, and the circulation likewise, by means of artificial respiration. Lastly, it is equally notorious, that if venous blood be withdrawn from the body and exposed to the atmosphere, it becomes rapidly arterialized, and carbonic acid is simultaneously generated. It must be here observed, that if I seem to judge of arterialization by the change of colour, I am only using the same criterion as M. Dupuytren himself; any further changes are alike unknown to M. Dupuytren and his opponents, and no reasoning can therefore be founded upon functions of which all physiologists are equally ignorant. For these reasons, then, in particular, and still more from analogy in other animals and in plants, I am strongly of opinion, that neither the eighth pair, sympathetic, or any other nerve, exerts any direct influence upon the function of respiration properly so called.

But it will now be asked, if the eighth pair of nerves have no influence upon the real function of respiration, what is the influence which it does possess? Whence is it that when these nerves are divided, animals invariably die? Or whence is it that the destruction of the medulla oblongata instantly puts a stop to respiration, and terminates life? To this, I have little hesitation in replying, that injuries to the medulla oblongata, from which the par vagum originates, and to that nerve itself above the origin of the superior laryngeal nerve, destroy life, not by checking any supposed function of the lungs themselves, but simply by closing the air-passages, and thereby preventing that preliminary condition, without which, in mammalia, respiration is impossible. It is not respiration, therefore, but the mecha-

* See "Wilson Philip on the vital functions."

† Id.

nism of respiration, which is thus destroyed. When the eighth pair, on the contrary, is divided below the origin of the laryngeal nerve, I am strongly of opinion, that the loss of the sensation which prompts us to respire, and which dictates to us when to renovate the air, in the same manner as the cravings of hunger impel us to seek the means of subsistence, is the real cause of the imperfect respiration which follows, and which soon terminates in death. When an infant is suffering from hunger, and applied to the breast of its mother, instinct teaches it the means of alleviating its distress ; but destroy that sensation, and the instinct is lost. Thus it is, I believe, with the animal in the condition alluded to : no longer incommoded with the sensation that warns him to respire, his respiration becomes no longer an object of attention : from habit it may continue for a time, but becoming more and more imperfect as the venous blood accumulates in the lungs, it ultimately ceases altogether, because the animal is no longer prompted to the efforts which would restore arterialization ; for the admonitory sensation being lost, instinct no longer teaches him to employ them. On what other principle than this, is death from coma to be satisfactorily explained ? It is true that consciousness and sensation are lost, but does the heart's action therefore cease ? We know that it will beat independently of these causes, and that its pulsations continue for a time, even after the individual has ceased to respire. Is it not, therefore, obvious, that it is the respiration that ceases, because consciousness and sensation are lost, and that the cessation of the action of the heart is subsequent to, and consequent upon the cessation of respiration ? And to what nerve are we to refer this connection of respiration with sensation, if not to the par vagum, whose lesion is found to be so fatal to that function ? Be it observed, that I do not here intend to discuss the distinction between voluntary and instinctive respiration ; that is foreign to the argument, for whether respiration be voluntary or instinctive, both the

will and the instinct are in coma alike destroyed. The former, directly, from the lesion of the brain in which it is supposed to reside ; the latter, indirectly, from the loss of sensation upon which instinct may be said to depend. In either case, there is in coma a loss of sensation, partial only while respiration continues, total when it ceases altogether.

The influence of the par vagum being thus explained, there is no difficulty in assigning their respective functions to the other nerves distributed to the different muscles of respiration ; their distribution shews obviously the purposes for which they were designed : it is, however, interesting to observe, as tending still more to demonstrate how little the real respiratory process is dependent on their influence, that those nerves which, next to the par vagum, are perhaps most important to respiration in mammalia, are of so little general distribution, that below this class they do not even exist. The phrenic nerve, for example, on which the respiratory movements in mammalia may be considered as mainly depending, is, together with the muscle to which it is distributed, entirely wanting in birds ; while the intercostal nerves, which are next in importance in the former class, are quite useless as regards respiration in the turtle, where the ribs are united, and in the batracians, where they are altogether wanting. On the other hand, the glosso-pharyngeal and ninth nerves, unknown as nerves of respiration in mammalia, are, in fishes, almost the only nerves with which the respiratory movements are connected ; and, lastly, in the invertebrate animals, in many of which little mechanism is required for this function, we have no proof of its dependence on any nervous influence at all. Surely, then, no further arguments are required to demonstrate, that a function which we find existing in full perfection, without a phrenic nerve, without intercostals, without a cerebro-spinal axis, and, lastly, without any vestiges of nervous matter whatever, is not essentially, but only incidentally, subjected to nervous influence.

Although somewhat foreign to the argument, it would be disrespectful to pass over in silence the opinions of a very eminent and enlightened physiologist, whose discoveries of the functions of the nervous system have rendered his name so deservedly illustrious. It is perhaps no disparagement to the genius of that distinguished individual to assert, that if, like Harvey, he has penetrated deeply into the mysteries of physiology, he has emerged, like his predecessor, resplendent indeed with the sun-beams of truth, but not totally unobscured by the mists of speculation; for whilst we find him demonstrating, with a perspicuity which carries conviction to every mind, the existence of distinct nerves for motion and sensation, we find him indulging in the most hypothetical speculations on the nerves of respiration, the truth of which, the evidence he adduces is surely insufficient to establish.

As I wish to touch briefly on this subject, I will only observe, that Sir Charles Bell's theory of a common centre or "tractus" for all the nerves connected with respiration, is, I conceive, liable to three grand objections. First, he is unable, by his own shewing, to trace any such tractus below the second or third cervical vertebra.* Secondly, supposing it to continue the whole length of the spinal marrow, he is unable to demonstrate any difference in the origin of the intercostals, and those cervical nerves which give origin to the phrenic, from those which form the axillary plexus; the two former being most important, as connected with the respiratory movements, the latter being wholly independent of them, and destined for a very different purpose. Thirdly, there are nerves traceable to his supposed "tractus," which are not connected with the respiratory apparatus, and which ought, therefore, consistently with his theory, to have an origin altogether dis-

* Bell on the Nervous System of the Human Body.

sociated from those which are concerned in the mechanism of this function.

Conclusions.

Having endeavoured, in the preceding pages, to trace the function of respiration, from one extremity to the other of the scale of organization, it now remains for me to explain, in conclusion, the inferences which I am inclined to deduce from this comparative survey.

First, "As to the uniformity of the function."

It appears from all that has preceded, that in every class of animals and vegetables, "the reciprocal action between " the constituents of the atmosphere and the organic " fluids," is essentially the same; that in all of them there is a disappearance of oxygen, and an evolution of carbonic acid; that simultaneously with this change in the constituents of the atmosphere, the organic fluids are likewise experiencing a change, the nature of which is imperfectly understood, but without which it is obvious that they are no longer fitted for supporting the life of the individual.

The *second* inference to be drawn from the foregoing observations, is—

"That the apparent deviations in this function, in some " of the departments of the scale, are not in kind, but " only in degree."

This inference is necessary to substantiate the former, but in order to establish it, it will be requisite to recall the reader's attention to some of these apparent deviations.

The first that occurs is in vegetable respiration. We have seen that, under certain circumstances, vegetables can apparently reverse the function, and replace carbonic acid with oxygen gas. Upon reflection, however, it will be found, that this is rather an additional function exercised by vegetables, than a deviation from that already

described. It only proves that vegetables can retain a portion of carbon extracted from the atmosphere, and that that element is to them a source of nutrition ; but it by no means demonstrates that oxygen is not essential to their existence. On the contrary, although a slight admixture of carbonic acid is an atmosphere favourable to vegetables, we have seen that if that admixture be such as materially to diminish the proportion of oxygen, vegetables as well as animals languish, wither, and die. A due supply of oxygen is therefore as necessary to vegetable as to animal life, and the result of its action is to produce such chemical or vital changes upon the fluids of plants, as to give rise to the evolution of carbonic acid.

The deviations in vegetable respiration are, therefore, not real, but apparent, and must be considered rather as super-added, than as vicarious functions.

The next apparent deviation in the function of respiration, is the tenacity of life exhibited by batracian reptiles, under circumstances where we should at first suppose respiration to be impossible. That it is quite possible, however, for the lungs to be excised, and respiration continue through the medium of the skin, is proved by the fact, that the air does actually undergo the usual respiratory changes, when animals thus treated are placed in it. There is here, therefore, no difference in kind, although, from one important organ being removed, there is a difference in degree of the respiratory function. The immersion of these animals in hydrogen, or other gases destitute of oxygen, is likewise only a demonstration of difference in degree ; for under these circumstances, they are deprived of oxygen, and they die ; being distinguished, however, from other animals, by requiring a less frequent renewal of that gas, and consequently by a capacity of enduring life for several hours, under treatment which, to those differently constituted, would prove almost instantly fatal.

Lastly, the existence of batracians, when enclosed in solid bodies, (wonderful as it appears,) does not disprove the necessity for respiration, but only shews that it can exist in an exceedingly low degree, and yet suffice for the life of the individual. The experiment, in which an animal was inclosed in solid plaster, and continued to respire until the atmosphere was totally excluded, is amply sufficient to demonstrate that, even under these circumstances, a certain degree of respiration is necessary to sustain existence. It must be remembered, likewise, that, in these situations, the body is protected from wasting ; that its loss by evaporation is extremely small ; that its corresponding supply is proportionably diminished, and there is no apparent vital energy remaining, except the power of resisting decomposition. Under these circumstances, it is evident that the circulating fluid, receiving the nutritive material extremely sparingly, undergoes a very slow and gradual vitiation, for which the most scanty supply of air, and the most feeble respiration, are amply sufficient to compensate. There is here, therefore, in all probability, no deviation in kind, but only in degree.

The *third* inference to be drawn from the preceding observations, may be regarded as a corollary to the first and second, viz.

“ That the function of respiration, in organized beings,
 “ having been shewn to be uniform throughout, and any
 “ deviation being not in kind, but only in degree, it fol-
 “ lows that any agency upon which this function can be
 “ allowed necessarily to depend, must itself likewise uni-
 “ formly exist ; and on the contrary, that if such existence
 “ be not uniform, but partial only, any necessary depen-
 “ dence of respiration on any such influence is both absurd
 “ and impossible.”

The *fourth* inference which remains to be deduced, and the correctness of which the preceding pages will, I think, sufficiently substantiate, is—

“ That a nervous system is of partial distribution, and
“ not uniform throughout the scale of organization.”

To this inference we are led, partly by the insufficiency of direct evidence, to establish its uniform existence ; but still more by the strong presumptive evidence derived from the effects of such a system, the phenomena of which are found to be totally wanting in a very numerous class of organic bodies.

Fifthly, “ These premises being admitted, it follows, as
“ a necessary consequence, that respiration being uniformly
“ present, and a nervous system not uniformly present,
“ respiration is not necessarily dependent on a nervous
“ system.”

Sixthly, and *lastly*, “ We must infer, from the foregoing facts, that although respiration be not necessarily dependent upon a nervous system, it may, nevertheless, be so circumstanced, with regard to its preliminary conditions, as to render the co-operation of nervous influence indispensable to its exercise ; such co-operation being, of course, variously modified, with the diversity of the mechanism to which it is subservient.”

GEORGE A. F. WILKS.

FINIS.

